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The enigmatic bovid *Duboisia santeng* (Dubois, 1891) from the Early–Middle Pleistocene of Java: A multiproxy approach to its paleoecology

Roberto Rozzi [a,*], Daniela Eileen Winkler [b], John De Vos [c], Ellen Schulz [b], Maria Rita Palombo [a,d]

[a] Dipartimento di Scienze della Terra, Università di Roma"La Sapienza", Piazzale Aldo Moro, 5, Roma, Italy
[b] Biocenter Grindel & Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, Hamburg, Germany
[c] Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands
[d] CNR, Istituto di Geologia Ambientale e Geoingegneria. Montelibretti (Roma), Italy

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ABSTRACT

During the Pleistocene, the Sunda Islands to which Java belongs were frequently connected with the East Asian mainland, permitting faunal elements of Indo-Chinese origin entering Java. Therefore, most Javanese mammalian taxa are close if not identical to their mainland relatives. In particular, three fossil bovids, commonly found in the Early–Middle Pleistocene "*Stegodon-Homo erectus* fauna" (*Bubalus palaeokerabau*, *Bibos palaesondaicus*, and *Epileptobos groeneveldtii*), do not show any feature consistent with the evolutionary pattern of typical insular mammals. However, a fourth Javanese bovid, *Duboisia santeng* has been regarded as a typical insular endemic species due to its small size. However, since *Duboisia* has been claimed to be present in the late Middle Pleistocene of what is now peninsular Malaysia, the actual endemic insular status of this taxon needs further confirmation.

In this study we aim to contribute to the debate by analyzing the autecology of Javanese *Duboisia santeng*, delving into its paleobiogeographic history and evolution. The multiproxy approach adopted here (body mass estimate, paleohabitat predictions, morphological comparison, mesowear analysis and Dental Areal Surface Texture Analysis DASTA) gave mutually consistent results and proved to be useful in supporting hypothesis regarding the complex evolution of insular faunas.

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1. Introduction

Java, one of the largest Indonesian islands, is famous for its fascinating fossil record (Van den Bergh et al., 1996; Widianto et al., 2001; Van Heteren and De Vos, 2012), which includes remains of the so-called "*Pithecanthropus erectus*" (nowadays called *Homo erectus*). During the Pleistocene, the Sunda Islands, to which Java belong, were frequently connected with each other and with the Southeast Asian mainland. During glacial phases the sea level dropped between about 50 and 200 m, resulting in the exposure of the Sunda Shelf (Voris, 2000). These temporary connections between the Sunda Islands and the Southeast Asian mainland permitted some faunal elements of Siva-Malayan origin, including bovids, to enter Java. Bovids are not so common in endemic Pleistocene insular faunas and are only recorded in Southeast Asia (Philippines), Japan (Ohdachi et al., 2009), and on some Mediterranean islands (Balearics, Sardinia, Sicily and perhaps Pianosa) (Palombo et al., 2006; Van der Geer et al., 2010; Palombo et al., 2013). Bovid diversity was, however, quite high in the Early–Middle Pleistocene of Java, including at least four species: *Bubalus palaeokerabau* (Dubois, 1908), *Bibos palaesondaicus* (Dubois, 1908), *Epileptobos groeneveldtii* (Dubois, 1908) and *Duboisia santeng* (Dubois, 1891) (Fig. 1). *B. palaeokerabau* was a large water buffalo or carabao, characterized by horn cores with a triangular cross section, which could reach a span of more than 2 m. *B. palaesondaicus*, a banteng-like bovine, had horn cores with an oval cross-section, curving backwards. *E. groeneveldtii*, was a leptobovine characterized by large horn cores, shifted farther behind the orbits, and a triangular occiput, with the upper angle formed by the parieto-occipital eminence. *D. santeng* was a small boselaphine with short and keeled horn cores (Hooijer, 1958; Bouteaux and Moigne, 2010), whose remains characterize the Trinil H.K. and Kedung Brubus Faunal units (Van den Bergh et al., 2001). In this study we aim to inquire into the autecology of *D. santeng* by applying several qualitative and quantitative methods (body-size estimation, paleohabitat predictions, morphological comparison, mesowear analysis and Dental Areal Surface Texture Analysis (DASTA). This multiproxy approach enabled us to better understand the paleoenvironment of Java at the time of the Trinil H.K. Faunal unit and provided us with some hints as to the paleobiogeographic history of the island.

* Corresponding author at: Dipartimento di Scienze della Terra, Sapienza Università di Roma, P.le Aldo Moro, 5, 00185 Roma, Italy. Tel. +39 0649914785.
E-mail address: roberto.rozzi@uniroma1.it (R. Rozzi).

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Fig. 1. Skull of the endemic bovid *D. santeng* from Java, lectotype of the species in frontal (on the left) and lateral view (on the right) (Trinil, Java). Naturalis Biodiversity Center (Leiden, The Netherlands).

1.1. Taxonomic background

The Dutch anatomist and paleoanthropologist Eugène Dubois, during his search on Java between 1890 and 1900 for the missing link between apes and *Homo* (his *Pithecanthropus erectus*; see Van Heteren and De Vos, 2012), retrieved the remains of a small bovid, quite different from those known at the time both from the mainland and the Sunda Islands. Dubois (1891) first described these remains simply as *Anoa* sp. and soon afterwards (1891) as *Anoa santeng*, ascribing them to the genus of the Sulawesi dwarf buffalo. Later (1907), he attributed the remains to the mainland genus *Tetracerus* and to the new endemic species *Tetracerus kroesenii*, stressing some affinities with Boselaphini. Stremme (1911) was the first to realize he was dealing with a new genus. Based on a well preserved skull (cf. Hooijer, 1958) found during the Selenka expedition (1907/08) at Trinil, he erected the genus *Duboisia* and attributed the material from Java to *Duboisia kroesenii*. As the species name "*santeng*" is a senior to the specific name "*kroesenii*" the correct name has to be *D. santeng*.

A few horn cores and teeth, similar in morphology and size to *D. santeng*, were retrieved by Cosjin (1931, 1932) from deposits of Eastern Java that he called the Jetis Beds. In 1934, Von Koenigswald established a new species, *Antilope modjokertensis*, on this material. According to this author (Von Koenigswald, 1940), two species of the genus *Antilope* would have inhabited Java contemporaneously with *D.* "*kroesenii*": *A. modjokertensis* and the slightly larger *Antilope saatensis*. An exhaustive description of the *Duboisia* material (skulls, teeth and horn cores) stored in the Dubois collection of the Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie and Rijksmuseum van Geologie en Mineralogie) was given by Hooijer (1958), who attributed the specimens of the Cosijn collection to *D. santeng*. In addition, Hooijer (1958) compared this species with the nilgai (*Boselaphus tragocamelus*) and the four-horned antilope (*Tetracerus quadricornis*), confirming the close affinity of *D. santeng* with these taxa, as already had been pointed out by Stremme (1911) and Pilgrim (1939). Later, Hooijer (1963) described some remains coming from the late Middle Pleistocene site of Tambun (today part of peninsular Malaysia; Tougard, 2001; Meijaard, 2004) as belonging to *D. santeng*. Should this attribution hold true, this species would not be endemic to Java as was generally believed (e.g. Van den Bergh et al., 2001; Joordens et al., 2009), but more widely diffused across the Sundaic province (Fig. 2).

Since the 1960s, the sample of Javanese *D. santeng* has been increasing thanks to several field excavations such as the ones at open-air sites in the Sangiran dome, which led to the discovery of *D. santeng* specimens in various localities (Tanjung, Ngrejeng Plupuh, Bukuran and Ngebung 2; Bouteaux and Moigne, 2010) (Fig. 2).

Three upper molars and a premolar, retrieved from the area around Bumiayu and from Sangiran, were ascribed by Geraads (1979) to a new species, *Duboisia* (*?*) *sartonoi* (= *Duboisia saatensis* von Koenigswald, 1934), but their attribution to the genus *Duboisia* is doubtful. These teeth, larger in size than those of *B. tragocamelus*, are characterized by "their hypsodonty and the simplicity of the upper molar occlusal pattern" (Geraads, 1979). Van den Bergh (1988) proposed the name *Duboisia problematicus* for a large skull fragment found in the area of Bumiayu, previously determined as *Cervus problematicus* by Von Koenigswald (1933). According to Van den Bergh (1988), the large teeth from Bumiayu and Sangiran would belong to this species, which he proposed to be the possible ancestor of *D. santeng*.

Although *D. santeng* has been recognized since the end of the 19th century, the taxonomy of some specimens and the phylogenetic relationships of the genus are still debated. Moreover, a full description of the postcranial elements was only given by Van den Bergh (1988), who confirmed the close relationship between *Duboisia* and *B. tragocamelus*. Pending a revision of the material attributed to *D. problematicus* and taking into account the number of features shared by *D. santeng* and *Boselaphus* (Stremme, 1911; Matsumoto, 1918; Pilgrim, 1939; Hooijer, 1958; Van den Bergh, 1988) and the similarities between the "*Stegodon-H. erectus* fauna" of Java and the Pinjor fauna from the Siwaliks (De Vos, 1996; De Vos and Long, 2001), the assumption that *B. namadicus* of the Siwaliks would be the ancestor of *D. santeng* seems the most plausible.

2. Materials and methodology

Most of the specimens of *D. santeng* in this study – more than 150 – belong to the Dubois collection of the Naturalis Biodiversity Center (Leiden, The Netherlands) and were collected from various sites on Java (Trinil H.K. and Kedung Brubus Faunal units; Dubois, 1891; Hooijer, 1958; Van den Bergh, 1988; Bouteaux and Moigne, 2010 (Fig. 2) (see Supplementary Material 1 for a list). A few teeth used for body mass estimations come from the Academy of Natural Sciences of Philadelphia (Von Koenigswald collection unpublished material). Specimens collected from various sites on Java were used for body mass estimates, while dietary reconstructions and paleohabitat predictions were performed on well preserved available remains coming from Trinil H.K. Specimens of *B. tragocamelus* used for morphological comparison are stored at the Natural History Museum (London, UK).

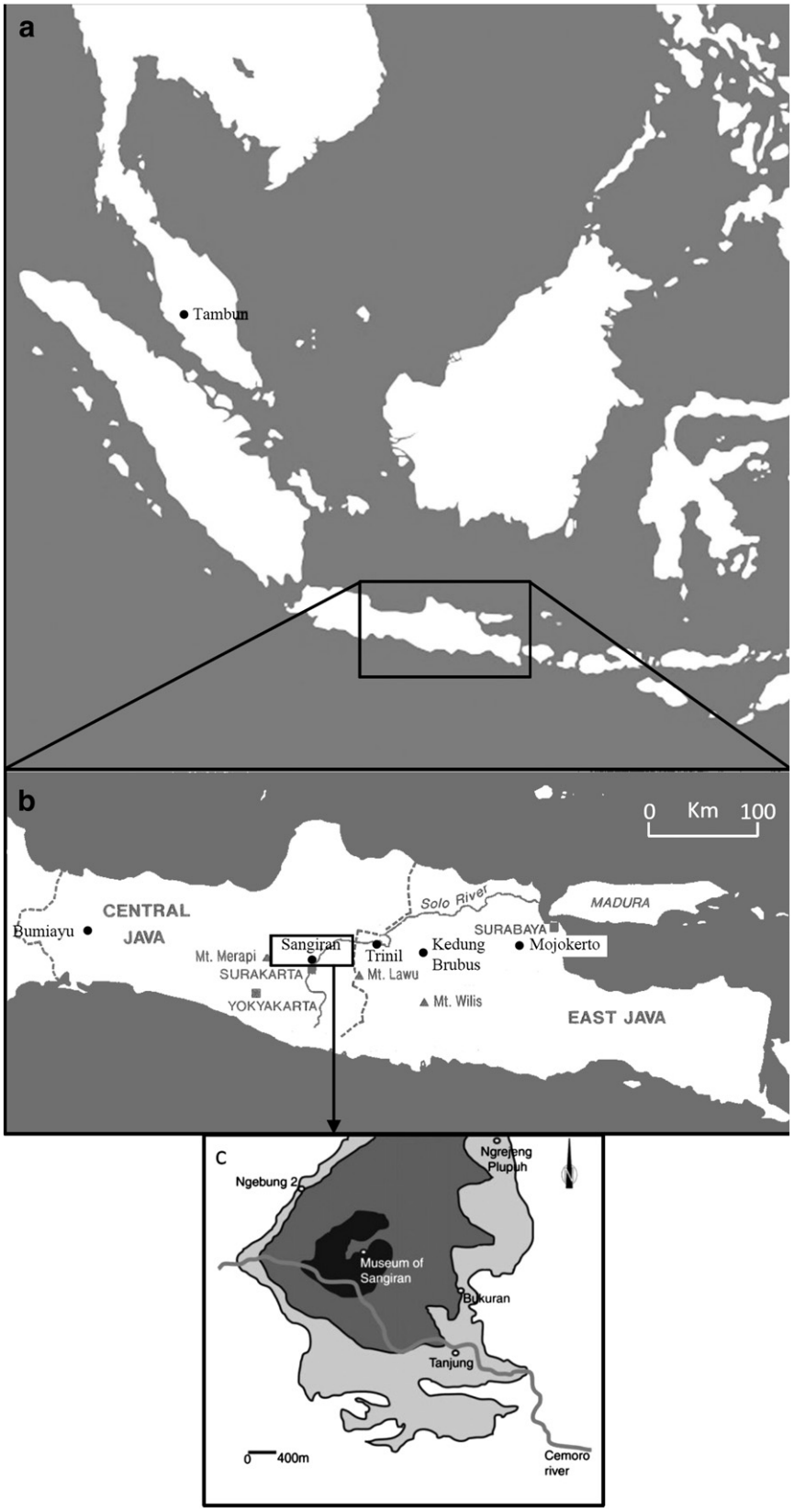


Fig. 2. Map of the main localities of *Duboisia* findings across the Sundaic province. Modified from Van den Bergh et al. (1996) and Bouteaux and Moigne (2010).

Qualitative and quantitative analyses in this study were performed only on adult specimens and measurements were recorded to the tenth of a millimeter. In particular, adult individuals with wear facets present on the upper third molar (M3) were selected for dietary reconstruction in order to gain a consistent age structure in the sample.

2.1. Body mass estimate

Body size may be regarded as a central aspect of mammal adaptive strategy, since it is strictly related to animal architecture and physiology, ecology and ethology (e.g. Hutchinson and MacArthur, 1959; McNab, 1971, 1990; Van Valen, 1973; Schmidt-Nielsen, 1975; Eisenberg, 1981; Janis, 1982; Robinson and Redford, 1986; Alexander et al., 1988; Palombo, 2009; Lomolino et al., 2012, in press). Body mass has been considered the best proxy of body size (Gingerich et al., 1982) and different allometric equations (based on cranial, teeth or long bones dimensions) have been proposed to estimate the body mass of fossil species (see *inter alios* Anderson et al., 1985; Van Valkenburgh, 1988; Damuth and MacFadden, 1990; Janis, 1990; Alberdi et al., 1995; Martinez and Sudre, 1995; Delson et al., 2000; Palmqvist et al., 2002; Giovinazzo, 2003; Christiansen, 2004; Palombo and Giovinazzo, 2005; Mendoza et al., 2006; De Esteban-Trivigno and Köhler, 2011). The body mass of *D. santeng* was estimated by using the predictive equations with the lowest predictive errors among those based on dimensions measurable on the available specimens (Table 1), then averaging all the obtained body masses. In order to infer the size shift of *D. santeng* in light of the island rule, its relative size was expressed as a proportion of the body mass of its putative mainland ancestor (Si = body size divergence, *sensu* Lomolino, 2005). The estimate rests on the assumption that *B. namadicus* from Siwaliks would be the ancestor of *D. santeng* (see above) and that its body mass would not differ significantly from that of its extant relative *B. tragocamelus*. Indeed, the size of *B. namadicus*, estimated on the scanty available material (two incomplete large skulls stored in the Natural History Museum of London, UK), is 238 kg (average value) and corresponds to the one of the largest individuals of *B. tragocamelus* (range of mass: 120 to 240 kg; Gozdzik, 2001). This is the reason why we decided to use also the average value of the body mass of living *B. tragocamelus* in order to obtain another estimate of Si, in addition to the one calculated on the basis of the scanty remains of *B. namadicus*.

2.2. Dietary reconstruction: mesowear analysis and Dental Areal Surface Texture Analysis (DASTA)

Dietary reconstruction of extinct species based on tooth wear can be performed on different scales. Microwear analysis uses microscopic wear features such as pits and scratches on enamel facets and has been used for dietary inferences for more than five decades (Baker et al., 1959; Walker et al., 1978; Teaford, 1988). It can be performed on high or low magnification (Solounias and Semprebon, 2002; Semprebon et al., 2004). More recently, 3D approaches to quantify enamel wear features such as Scale-Sensitive Fractal Analysis SSFA (Ungar et al., 2003; Scott et al., 2005, 2006; Ungar et al., 2007) and DASTA (Calandra et al., 2012) have proven to be powerful tools, as they rely on unbiased computer-generated parameters rather than on subjective counting of wear features (Schulz et al., 2010, 2013a,b).

The mesowear method after Fortelius and Solounias (2000) evaluates wear patterns on ungulates teeth visible with the naked eye or with only minor magnification. Mesowear analysis is based on facet development of postcanine teeth. Facets are created by attrition (tooth-to-tooth-contact) while abrasion (tooth-to-food-contact) obliterates them. The resulting wear pattern is described by two variables, occlusal relief and cusp shape, which are scored in the following categories on the buccal side: Occlusal relief can either be high or low, cusp shape is scored as sharp, round or blunt (Fig. 3).

We applied both the mesowear method and Dental Areal Surface Texture Analysis DASTA. Mesowear can be quickly analyzed and gives a reliable classification into the broad dietary categories of browser, mixed feeder and grazer. DASTA, on the other hand, is based on standardized industrial surface parameters and provides implications on the material properties of the food consumed.

All teeth were cleaned and molded with Provil novo Light C.D. fast set EN ISO 4823, 13 type 3, light (Heraeus Kulzer GmbH, Dormagen, Germany), a standard procedure often described in literature (Fortelius and Solounias, 2000; Rivals and Semprebon, 2006; Kaiser and Rössner, 2007). Positive castings of the silicone molds were made with epoxy resin (Injektionsharz EP, Reckli-Chemiewerkstoff, Herne, Germany) and were used in both analyses. We obtained data from 13 individuals for mesowear analysis and 8 individuals for DASTA.

For DASTA, surface scans of enamel facets were obtained using the high resolution disc-scanning confocal 3D surface measuring system μsurf Custom (NanoFocus AG, Oberhausen, Germany) following the procedure in Schulz et al. (2010). For all measurements, a square area of 160 × 160 μm was scanned using the 100× long distance lens with a resolution in x, y = 0.16 μm and z = 0.06 μm. Surface areas with defects or adherent dirt were rejected, as well as measurements with less than 95% surface points recorded or a vertical displacement range $\delta z > 40$ μm. Up to four non-overlapping measurements per facet were scanned for each specimen when possible. Data were analyzed using Dental Areal Surface Texture Analysis (DASTA) applying the industrial texture standard ISO/FDIS 25178-2 after Schulz et al. (2010), Calandra et al. (2012), Schulz et al. (2013a) and Schulz et al. (2013b). DASTA is based on 3D industrial area surface texture standards (ISO/FDIS, 25178-2, 2010). It was conducted using μsoft analysis premium v.5.1 software (NanoFocus AG, Oberhausen, Germany; a derivative of Mountains® Analysis software by Digital Surf, Besançon, France). The original 3D surface models were first processed with implemented tools of μsoft analysis premium v.5.0 software according to Schulz et al. (2010). Thirty 3D-surface roughness parameters from the following classes of ISO/FDIS 25178-2 parameters were computed: 1. standardized height; 2. spatial; 3. hybrid; 4. functional; and 5. segmentation parameters (compare Schulz et al., 2010, 2013a,b).

Statistical analyses were carried out following Calandra et al. (2012) and using the open-source software R v. 2.13.2 (R development Core Team, 2009). The following packages were used for data mining and processing: doBy (Højsgaard, 2010), plyr (Wickham, 2010), RODBC (Ripley and Lapsley, 2009), RSvgDevice (Luciani, 2009), R.utils (Bengtsson, 2010), xlsReadWrite (Suter, 2010).

Table 1
Main equations used to calculate body mass of *D. santeng*.

Variable	R2	Reference
Astragalus area	0.95	Martinez and Sudre (1995)
Femur head area (FHA)	0.988	Kappelman (1988)
Several variables on limb bones	0.9203:0.9629	Scott (1990)
Several variables on skull and teeth	0.9340:0.9520	Janis (1990)
Several variables on limb bones	0.9056:0.9184	Giovinazzo (2003)
Width of occipital condyles (WOC)	0.83	Palombo et al. (2006)

2.3. Limb bones as paleohabitat predictors

Several methods have been developed to use bovid postcranial elements in the functional morphology approach to paleohabitat prediction (Kappelman, 1988; Plummer and Bishop, 1994; Kappelman et al., 1997; DeGusta and Vrba, 2003, 2005a,b; Kovarovic and Andrews, 2007; Weinand, 2007; Plummer et al., 2008; Klein et al., 2010). In this study we analyzed different limb bones of *D. santeng* and *B. tragocamelus*, combining an eco-morphological comparative analysis of femur, phalanges and metapodials (Kappelman, 1988; Köhler, 1993) with a variety of morphometric methods, based on astragalus and femur dimensions. The femur is among the postcranial elements that have been proven as useful in past habitat reconstructions of extant and extinct bovids due to the variation of some functional features, according to locomotor patterns across the habitat spectrum (Gentry, 1970; Kappelman, 1988; Kappelman et al., 1997). For example, bovids with a more rounded *caput femoris* and with a more proximally and centrally situated fossa of the *ligamentum* reflect a pattern of locomotion requiring maneuverability and a great degree of abduction

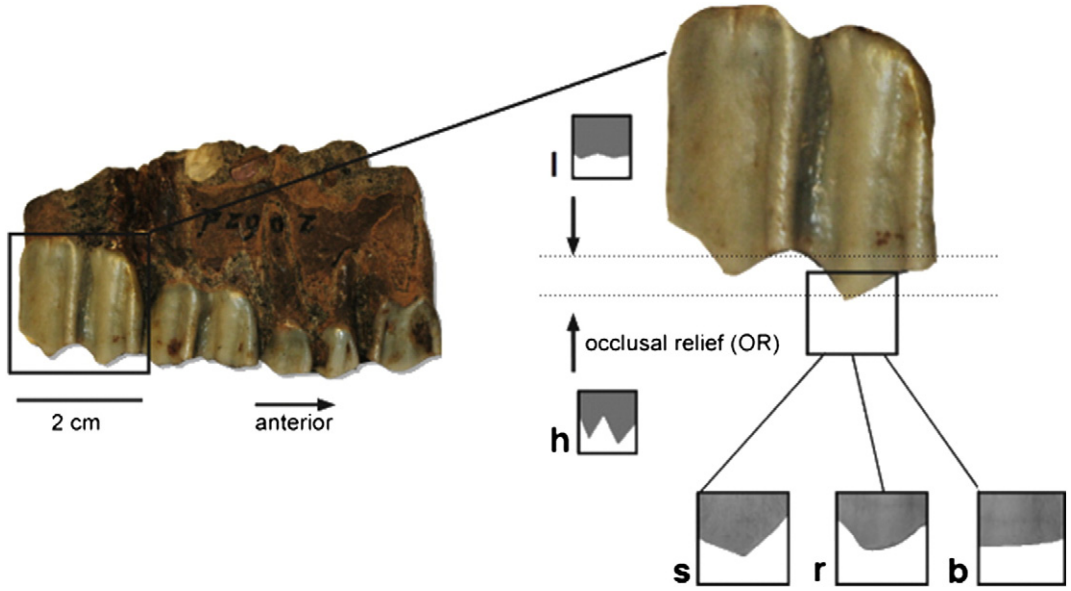


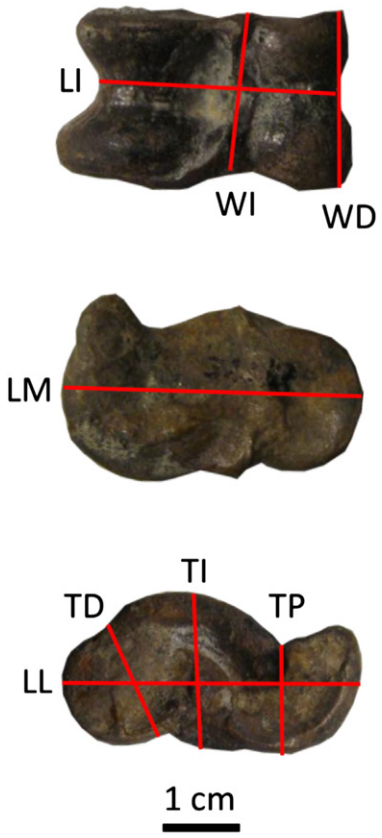
Fig. 3. The mesowear scoring convention – as defined by Fortelius and Solounias (2000) for upper second molars of ungulates – on a specimen (2062d) of *D. santeng*. Occlusal relief (OR) may be scored as "high" (h) or "low" (l); cusp shape (CS) is classified as "sharp" (s), "round" (r), or "blunt" (b).

and axial rotation at the hip. This adaptation characterizes bovids living in closer canopy settings, which often face a complex, nearly three-dimensional substrate of tree trunks, shrubs, roots, and bushes, all of which could affect high-speed cursorial locomotion, to a great extent. At the other end of the habitat spectrum are species living in open habitats where ground-level obstacles may only occasionally be present. These bovids have a femoral head that is more cylindrical in shape and acts to limit movements to the parasagittal plane, while the morphology of the distal part of the femur determines a large moment arm for the extensor tendons (Kappelman, 1988; Kappelman et al., 1997). Measurements of the femur useful for distinguishing among bovids from different habitats were taken on the focal specimens of *D. santeng* following Kappelman (1988) and Kappelman et al. (1997) and were compared with the large database of extant bovids (38 species) in Kappelman et al. (1997). Only the most significant femoral variables, such as FHA (= femoral head area) and others showing either a clear increase (FHSS = femoral head shape score; LTR = lesser trochanter anteroposterior: mediolateral ratio; PSR = proximal anteroposterior: mediolateral shaft ratio) or decrease (PHR = patellar lip height ratio; MPLR = medial patellar lip ratio) in magnitude with increasingly closed conditions, were used in this study (Table 2). Four general categories of habitat were used: the 'Forest' category includes, naturally, forest dwelling taxa (scrub-forest, forest, rainforest); 'Heavy Cover' category includes taxa which live in bush, woodland, swamp, and near-water habitats; 'Light Cover'category gathers taxa that inhabit light bush, tall grass, and hilly areas and 'Open' category is that of taxa living in edge or ecotone, open country, and arid country (Kappelman et al., 1997; DeGusta and Vrba, 2003, 2005a).

Astragali and phalanges have been chosen among those bones regarded as the most accurate in inferring paleohabitats (DeGusta and Vrba, 2003, 2005a; Weinand, 2007; Rozzi and Palombo, in press). As the number of available phalanges of *D. santeng* is not statistically significant, we focused on astragali. Measurements, recorded to the tenth of a millimeter, were taken following DeGusta and Vrba (2003) (Fig. 4). Although biomechanical data linking between astragalus morphology and locomotion are currently not available in the literature, a general indication of the morphological differences between habitat groups was provided by DeGusta and Vrba (2003). Measurements were used to predict habitat preference category (Forest, Heavy Cover, Light Cover, Open) by means of a discriminant function, generated by DeGusta and Vrba (2003; 2005a) using the statistics software JMP and based on a large database of extant African bovids, including 39 species

Table 2
Description and abbreviations of measurements of femora, following Kappelman (1988) and Kappelman et al. (1997).

Variable	Description
Femoral head shape score (FHSS)	Femoral head shape was scored on the distribution of articular area in the cranial projection andmeasured the taper of the femoral head along the mediolateral axis.
Femoral head area (FHA)	Area (cm^2) was calculated from a simple geometric construction of the superior view of the femoral head articular surface (see Kappelman, 1988).
Lesser trochanter anteroposterior:mediolateral ratio (LTR)	The anteroposterior and mediolateral dimensions at the lesser trochanter were measured withdial calipers. This ratio describes the morphology of the proximal femur at the distal margin of the intertrochanteric fossa.
Proximal anteroposterior:mediolateral shaft ratio (PSR)	The anteroposterior and mediolateral dimensions of the proximal shaft at the base of the lesser trochanter were measured with dial calipers. The ratio provides an estimate of the loading forces that operate through the proximal shaft.
Patellar lip height ratio (PHR)	The anteroposterior heights of the medial and lateral patellar lips to the respective femoral condyles were measured perpendicular to the shaft with an osteometric board. The ratio describes the relative symmetry of the distal femur.
Medial patellar lip ratio (MPLR)	The distance from the medial patellar lip to the femoral condyle in the anteroposterior plane, and the distance from the center of the patellar groove to the intercondylar notch were measured perpendicular to the shaft with an osteometric board and a dial calipers, respectively. The ratio of the medial patellar lip height to the distal AP shaft diameter estimates the relative moment arm of the extensor muscles that cross the knee.



Astragalus	
Medial length (**LM**): The maximum proximal–distal dimension of the medial surface taken parallel to the main proximal–distal axis of the astragalus.	Distal width (**WD**): The medial–lateral dimension of the distal end at its distal-most point.
Intermediate length (**LI**): The minimum proximal–distal dimension of the astragalus, taken parallel to the main proximal–distal axis of the bone.	Proximal thickness (**TP**): The anterior–posterior dimension of the proximal end of the lateral surface.
Lateral length (**LL**): The maximum proximal–distal dimension of the lateral surface taken parallel to the main proximal–distal axis of the astragalus.	Intermediate thickness (**TI**): The minimum anterior–posterior dimension of the lateral surface in the area of the junction between the proximal and distal articular regions.
Intermediate width (**WI**): The minimum medial–lateral dimension on the anterior surface in the area of the junction between the proximal and distal articular regions. Any projections or tubercles are included.	Distal thickness (**TD**): The anterior–posterior dimension of the distal end of the lateral surface.

Fig. 4. On the left, astragalus metrics on a specimen of *D. santeng* (3238B). On the right, description and abbreviations of measurements of astragali, following DeGusta and Vrba (2003).

and 218 individuals. While the equation assigns the studied elements to habitat groups in a statistical manner, it is also appropriate to have a sense of the morphological differences that permit this sorting. Therefore, scatter plots of dimensions of astragali for the specimens in the study were built. Finally, we carried out principal component analyses (PCA) on the list of measurements in Fig. 4 – using JMP (version 9; SAS Institute Inc., Cary, NC, 2009) software and the database of extant African bovids completed by DeGusta and Vrba (2003) – to delve into the clustering of specimens of *D. santeng* and further investigate the structure of the data.

3. Results

3.1. Body mass and body size divergence

Regression equations produced an average body mass estimate of 51.18 kg for the specimens from Trinil H.K. Body mass estimates obtained for the specimens found at Kedung Brubus fall within the range of values calculated for Trinil H.K., although the average value obtained for the most recent site is slightly higher (60 kg). As for the scanty remains found in other sites included in the sample, we obtained similar body mass estimates. All in all, taking into account the complete sample, the regression equations used produced body mass estimates ranging from about 32 kg (minimum 25 percent quartile) to about 84 kg (maximum 75 percent quartile), with an average value of 53.75 kg (Fig. 5). Given the variability in estimates derived from individual measurements in living taxa, this estimate is probably within 15% of the true mass of this fossil animal (Scott, 1983). The range of body mass values of *D. santeng* obtained from each predictive equation is reasonable, especially if compared with the ones of several extant small and middle sized bovids, such as *Ovis dalli* (range mass: 46 to 113 kg; Gozdzik, 2001), *T. quadricornis* (range mass: 15 to 25 kg; Gozdzik, 2001), *Alcelaphus buselaphus* (range mass: 75 to 200 kg; Gozdzik, 2001).

The relative size of *D. santeng* (body size divergence, Si) indicates an average body size reduction of about 77% (Si = 0.23%) with respect to the putative ancestor *B. namadicus*. A more parsimonious estimate, calculated with respect to *B. tragocamelus*, indicates an average body size reduction of about 70% (Si = 0.2985), with a minimum of about 65% (Si = 0.35) and a maximum of about 73% (Si = 0.2667).

3.2. Dietary reconstruction

The mesowear signature of *D. santeng* is rather uniform (Table 3). It is characterized by high and sharp profiles (70%), with a few rounded cusps (15%) and low/round profiles (15%). No blunt cusps are present. Therefore, *Duboisia* lies within the attrition dominated region of the mesowear equilibrium. The high frequency of sharp cusps in combination

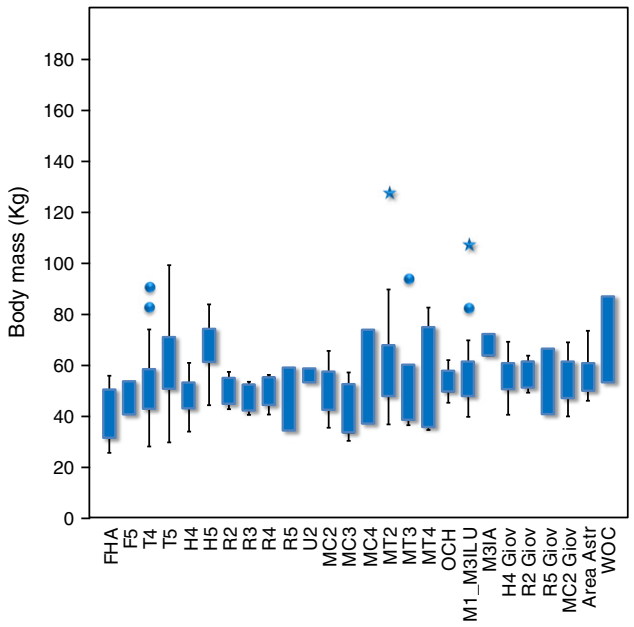


Fig. 5. Box plot summarizing the results of body mass estimates of *D. santeng*. For each predictive equation used, the 25–75 percent quartiles are drawn using a box, the minimal and maximal values are shown with short horizontal lines ("whiskers"). The whiskers are drawn from the top of the box up to the largest data point less than 1.5 times the box height from the box (the "upper inner fence"), and similarly below the box. Values outside the inner fences are shown as spheres, values further than 3 times the box height from the box (the "outer fences") are shown as stars. See Supplementary Material 2 for description and abbreviations of variables on which each predictive equation is based.

with high profiles and a lack of blunt cusps are characteristic of browsing ungulates. All in all, the mesowear signature with a small number of rounded cusps indicates a browsing feeding regime mostly typical for a forest dweller feeding on leaves, occasionally including abrasive vegetation to a minor extent.

This interpretation is well supported by results of DASTA (the parameter values are given in Table 3). *Duboisia santeng* has enamel texture surfaces with low roughness (*Sa*) and low density of peaks (*Spd*). Both volume parameters, core material volume (*Vmc*) and material volume (*Vm*) are also relatively low.

3.3. Locomotion and paleohabitat inferences

Morphological comparison show that *D. santeng* shares several features with typical extant forest dwellers, among which its extant relative *B. tragocamelus*. As regards the femur, one of the most useful bones in past habitat reconstructions, the Javanese bovid show a marked vertical inclination of the cranial articular surface of the femoral head with respect to the vertical axis of the shaft, a quite rounded *caput femoris* with a proximally and centrally situated fossa of the *ligamentum* and an overall symmetry of the patellar lips in distal view. These features characterize taxa requiring maneuverability and a great degree of abduction and axial rotation at the hip and they are, therefore, shared by *B. tragocamelus* and a typical forest dwelling morphological type (Kappelman, 1988; Köhler, 1993) (Fig. 6). In particular, the morphology of the *caput femoris* of *D. santeng* corresponds with morphological types A_1 and A_2 defined by Köhler (1993), which are regarded as typical for taxa living in from moderately to very humid wooded, and semiaquatic habitats (Fig. 6).

A number of ecomorphological features of metapodials are in agreement with the preferred habitat inferred by femur morphology. *D. santeng* is characterized by distally broadening metapodials, showing a triangular outline of their distal part, low distal articular surfaces and a long and well developed furrow for the lateral extensor tendon. These features (A, A_1 and A_2 in Köhler, 1993; Fig. 6) are typical of taxa living in wooded, from moderately to very humid habitats and are shared, among others, by *B. tragocamelus*. It is worth noting that metapodials of *D. santeng* are elongated and quite slender. The morphology developed by limb bones of the Javanese boselaphine somehow mirrors the one developed by Plio-Pleistocene Sardinian bovids (Palombo et al., 2006; 2013). The latter, being forced to escape the

Table 3
Parameter values of mesowear analysis (above) and DASTA (below). See main text for abbreviations.

Specimen ID	Bone	Side	OR	CSA	CSF
Dub-2062.c	txM2	r	h	s	s
Dub-2062.c	txM3	r	h	–	s
Dub-2062.d	txMl	r	I	r	r
Dub-2062.d	txM3	r	h	s	S
Dub-2055	txM2	I	I	r	r
Dub-2055	txM3	I	h	r	s
Dub-2062.b	txM2	r	h	–	s
Dub-2062.b	txM3	r	h	s	_
Dub-2062.a	txMl	r	h	s	r
Dub-2062.a	txM2	r	h	s	r
Dub-2062.a	txM3	r	h	s	s
Dub-2520.b	txM2	I	h	s	s
Dub-2056.a	txMl	I	h	s	_
Dub-2056.a	txM2	I	h	r	_
Dub-2056.a	txM3	I	h	s	_
Dub-13028	txM2	I	h	r	r
Dub-13028	txM3	I	h	–	s
Dub-2520.a	txM2	r	I	r	r
Dub-2520.a	txM3	r	h	–	s
Dub-1824.p	txMl	r	h	s	r
Dub-1824.p	txM2	r	h	s	s
Dub-13028-III	txM2	I	h	s	s
Dub-13029	txM2	r	h	s	s
Dub-13028-V	txMl	r	h	s	s
Dub-13028-V	txM2	r	h	–	s

ISO-parameter	*Sa*		*Spd*		*Vmc*		*Vm*	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
D. santeng	0.6672	0.3498	0.0012	0.0022	0.7324	0.3895	0.0378	0.0213

top predator running hyena, were characterized, conversely to the most of insular artiodactyls, by slender metapodials, as shown by the similar values of the robusticity index (robusticity index = 0.097 for the metatarsal of *D. santeng* 8465; robusticity index = 0.1 for the metatarsal of *Nesogoral* VI 3 Antica 1045 A Fig. 7).

Although only two not perfectly preserved proximal phalanges of *D. santeng* are present in the Dubois collection, they are quite robust and share many features with typical forest dwellers (type A in Köhler, 1993) (Fig. 6). The best preserved specimen (5918k, Fig. 6) shows a very rough surface of the internal side, marking the insertion of a strong interdigital ligament, a dorsally extended distal articulation, well visible in dorsal view, and a concave volar curvature beginning from the middle of the shaft. *D. santeng* is characterized by a rather strong intermediate phalanx, with a proximal volar end showing strong marks for the origin of the interdigital ligaments and the insertion of the *flexor digitorum superficialis* (type A in Köhler, 1993; Fig. 6). As regards the terminal phalanx, *D. santeng* shares with *B. tragocamelus* and typical forest dwellers (type A in Köhler, 1993; Fig. 6) a triangular outline in lateral view, an almost straight dorsal ridge and the absence of a special process for the insertion of the extensor tendon.

Results obtained by biometric analysis are quite consistent with evidence resulting from morphological comparison. Ranges of variability of each femoral score for every habitat group highlight a morphological trend across the habitat spectrum from closed to open landscape in extant bovids (Kappelman, 1991). In particular, the need of great maneuverability of typical Forest dwellers is marked in functional terms by a more spherical shape of *caput femoris* (high FHSS = femoral head shape score), a greater moment arm for the external rotators of the hip (high LTR = lesser trochanter anteroposterior:mediolateral ratio), a cross-section of the diaphysis that, in part, reflects greater anterior-posterior directed loading forces transmitted through the femoral head to the proximal shaft (high PSR), and a lower moment for extension at the knee (low MPLR, PHR). As regards *D. santeng*, values obtained for FHA fall within the range of extant Forest dwellers, although this variable shows an overlap of all the habitat categories (Fig. 8). Most of the values obtained for FHSS and MPLR fall just outside the ecospace of extant Forest dwellers, hypothetically suggesting a more extreme adaptation to wooded environments (Fig. 8). Values of PHR and LTR obtained for the Javanese bovid share a similar pattern, with most of the specimens falling within the overlapping range of extant Forest, Heavy Cover and Light Cover dwellers, while a few of them falling within the overlapping range of extant Heavy Cover and Light Cover dwellers (PHR, LTR) or outside the ranges of values characterizing the extant taxa (PHR) (Fig. 8). The value of PSR, unfortunately only available for a single specimen of *D. santeng*, falls within the overlapping range of extant Forest, Heavy Cover and Light Cover dwellers (Fig. 8).

The results of the statistical habitat prediction on astragali of *D. santeng*, summarized in Fig. 9, support the habitat assignment pointed out by means of morphological comparison and biometry. According to the discriminant functions, the majority of astragali (85.71%) would belong to taxa of the category "Forest", while a minimum fraction of the sample (14.38%) would belong to taxa included in the category "Light Cover".

These results are overall supported by plotting measurements of astragali (Fig. 9), despite an overlap of the ellipses representing 90% of each habitat group's distribution in the reference sample of modern

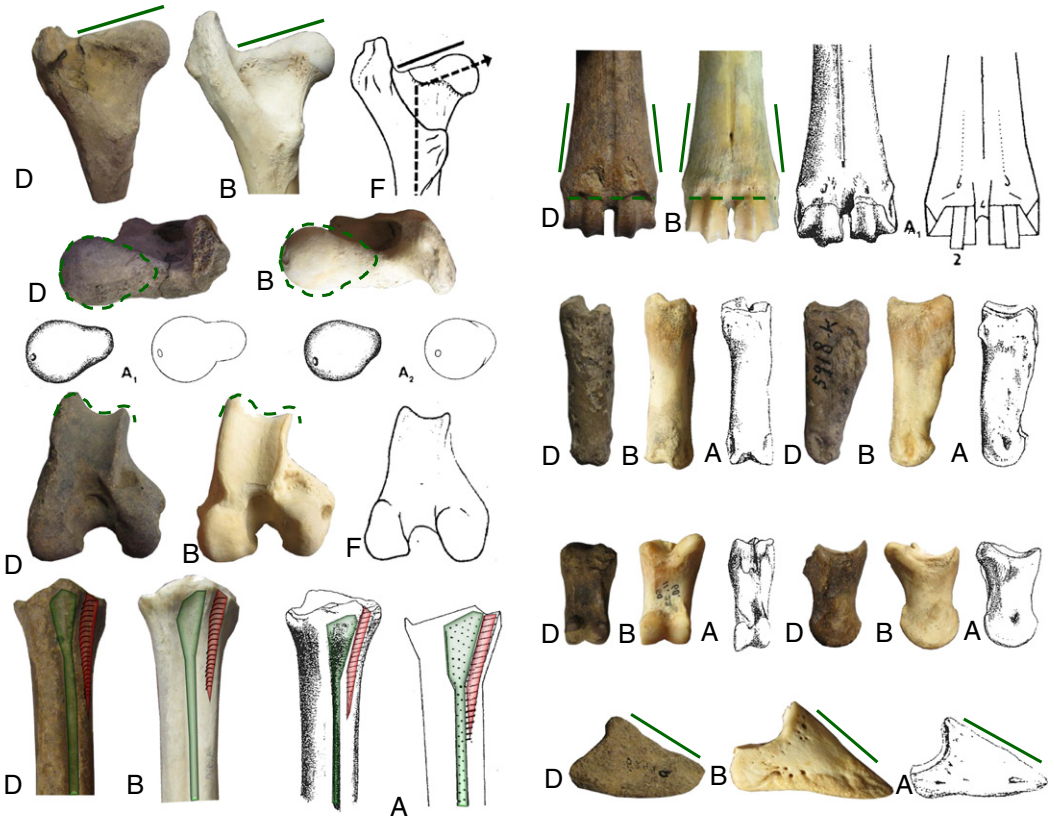


Fig. 6. Morphological comparison between postcranial elements of *D. santeng* (D), *B. tragocamelus* (B; specimen 1949.12.30.1 of the Natural History Museum of London), a typical forest dweller (F; following Kappelman, 1988) and types A, A_1 and A_2 in Köhler (1993); indicating types living in wooded habitats, from moderately to very humid. First three rows on the left: femora in caudal, proximal and distal views, respectively. Last row on the left: proximal part of metatarsals in dorsal view (shaded area: area for the Extensor tendons; parallel lines: furrow for the Lateral Extensor tendon). First row on the right: distal part of metacarpals in dorsal view. Second row on the right: proximal phalanges in dorsal and interdigital views. Third row on the right: intermediate phalanges in palmar and extern views. Last row on the right: terminal phalanges in extern view. Lines highlight typical features of forest dwellers (see Section 3).

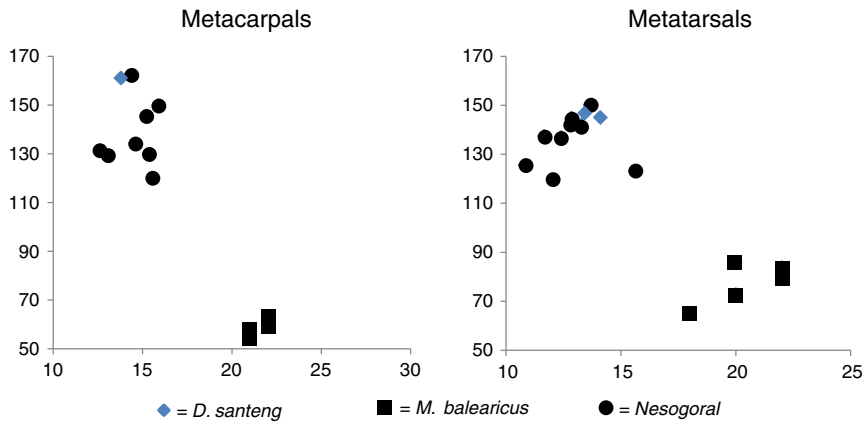


Fig. 7. Plot of robusticity index (medio-lateral diameter of the shaft and total length) of metapodials of *D. santeng*, *Nesogoral* (various morphotypes) from Monte Tuttavista and *M. balearicus* (measurements from Andrews, 1915).

African bovids (DeGusta and Vrba, 2003, 2005a; Rozzi and Palombo, in press). In fact, all the astragali of *D. santeng* herein examined fall within the Forest taxa ellipse, although six of them fall within the overlapping area of different categories.

As regards the results of the PCA (Fig. 10), the occurrence at the peripheric area of some isolated groups of Forest (e.g. *Madoqua* and *Neotragus*) and Open (e.g. *Taurotragus*) taxa highlights an increasing body size trend along the first component axis (explaining the 98.4% of the variability). In addition, this score plot shows the tendency of the specimens of *D. santeng* to form a quite condensed group, mostly falling into the third quadrant, containing small to medium sized Forest and Light Cover dwellers (Fig. 10). The dispersion of specimens along the second component axis is mainly related to differences in the intermediate width of the astragalus, for which we obtained the highest values in the PCA loadings.

All in all, results obtained by different methodological approaches are in agreement with each other. Dietary reconstruction of *D. santeng*, indicating that this taxon was a browser with some abrasive components to its diet, is indeed in agreement with morphology and paleohabitat predictions on the limb bones, suggesting an adaptation to forest settings often with complex nearly three-dimensional substrates. In particular, ecomorphological features on metapodials and femora enable us to infer that *D. santeng* inhabited wooded, from moderately to very humid habitats (see *B. tragocamelus* and types A, A_1 and A_2 in Köhler, 1993).

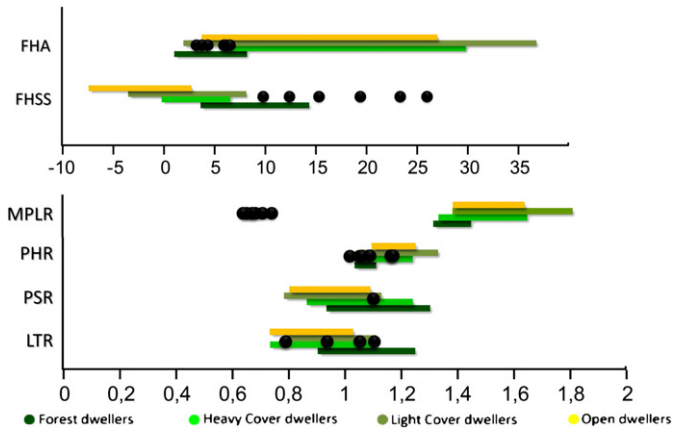


Fig. 8. Results of biometric analysis of femur. Ranges of variability of each score for every habitat group of the reference database of extant bovids (see Section 2) are denoted by colored bars. Specimens of *D. santeng* are denoted by black spheres. See Table 2 for measurement description and abbreviations.

4. Discussion

Different methodological approaches adopted in this study gave results in agreement with each other and this multiproxy approach proved to be useful in supporting hypotheses regarding the complex evolution of insular faunas, such as the one characterizing the Early–Middle Pleistocene of Java.

As for paleohabitat inferences, on the one hand our analysis confirm the general relationship between habitat and diet, with most grazers living in open habitats or savanna and most folivores and frugivores living in closed habitats or forests. On the other hand, it underlines the difficulties in firmly reconstructing paleoenvironment characteristics by inferring large mammal ecological traits. Species occurring at the extremes of the habitat spectrum are predicted to have locomotor adaptations that facilitate their foraging within their specific habitats. A high degree of cursoriality aids open country bovids in their foraging over great distances, while greater maneuverability facilitates food search in more closed habitat settings (Kappelman, 1988). Results obtained for *D. santeng* suggest that this species was a forest-dweller, mostly feeding on leaves and only occasionally on harder vegetation. In particular, results of both mesowear (see above) and DASTA indicate that this species was neither a grazer nor a pure frugivore, but a browser with some abrasive components to its diet. According to the results of DASTA, enamel surface textures are less rough (Sa) and voluminous (core material volume, Vmc) than in extant grazing ungulates, but slightly rougher than extant browsers (Schulz et al., 2013b), indicating a minor impact of abrasive particles which fracture the enamel surface. The density of peaks (Spd) in *D. santeng* is lower than in any other ungulate taxon measured so far (Schulz et al., 2013a,b; Winkler et al., 2013), but by trend *D. santeng* is closer to extant browsers. Based on the surface texture data of Calandra et al. (2012) *D. santeng* closely resembles the signature of extant browsers, as both grazers and frugivores have higher material volumes (Vm). Evidence regarding diet and habitat preference of *D. santeng* needs to be discussed in light of the complex and somewhat controversial reconstruction of the Javanese vegetational history.

Throughout the Early Pleistocene, Java was characterized by immense mangrove forests near the shoreline, while the neighboring elevations were covered by tropical rainforests during the 'interglacials', and a more open forest formation, although without the composition of an actual monsoon forest, during the 'glacials' (Sémah et al., 2010). During the late Early Pleistocene and at the transition to the Middle Pleistocene, the volcano-tectonic evolution of the island and the global climatic change resulted in a progressive rainforest fragmentation and the development of seasonal forests (Sémah et al., 2010). Although the climatic trend triggered the onset of an open vegetal cover towards a landscape dominated by grasslands, the forest formations, and especially

ASTRAGALUS					
Specimen	Predicted Habitat	Forest %	Heavy Cover %	Light Cover %	Open %
3238B	F	0,79	0,03	0,17	0,01
6925A	F	0,46	0,05	0,38	0,11
5079A	F	0,83	0,02	0,14	0
264A	F	0,65	0,04	0,29	0,02
264B	F	0,87	0,03	0,09	0,01
2178A	F	0,68	0,09	0,22	0
2178B	L	0,22	0,05	0,62	0,11
5797A	F	0,6	0,08	0,31	0,01
5797H	F	0,54	0,1	0,32	0,03
5797G	F	0,95	0,01	0,04	0
5797C	F	0,51	0,08	0,37	0,05
5797B	L	0,32	0,02	0,5	0,16
5797i	F	0,75	0,14	0,08	0,03
5797D	F	0,79	0,04	0,16	0,01

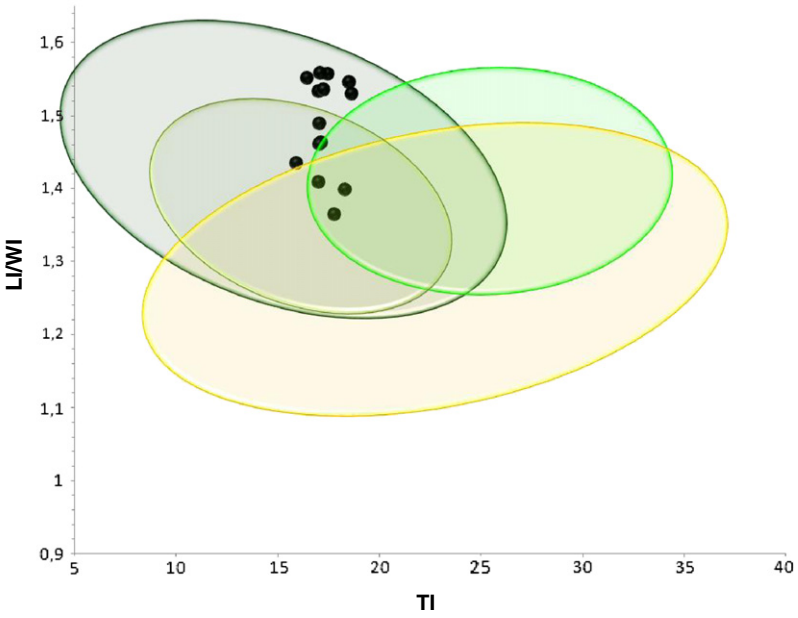


Fig. 9. Results of the statistical habitat prediction on astragali of *D. santeng* (on the left) and scatter plots of dimensions (see Fig. 4 for abbreviations) of astragali. Specimens of *D. santeng* are denoted by black spheres. The plotted measurements are regarded as the best in showing morphological differences between the bones of different habitat groups (DeGusta and Vrba, 2003).

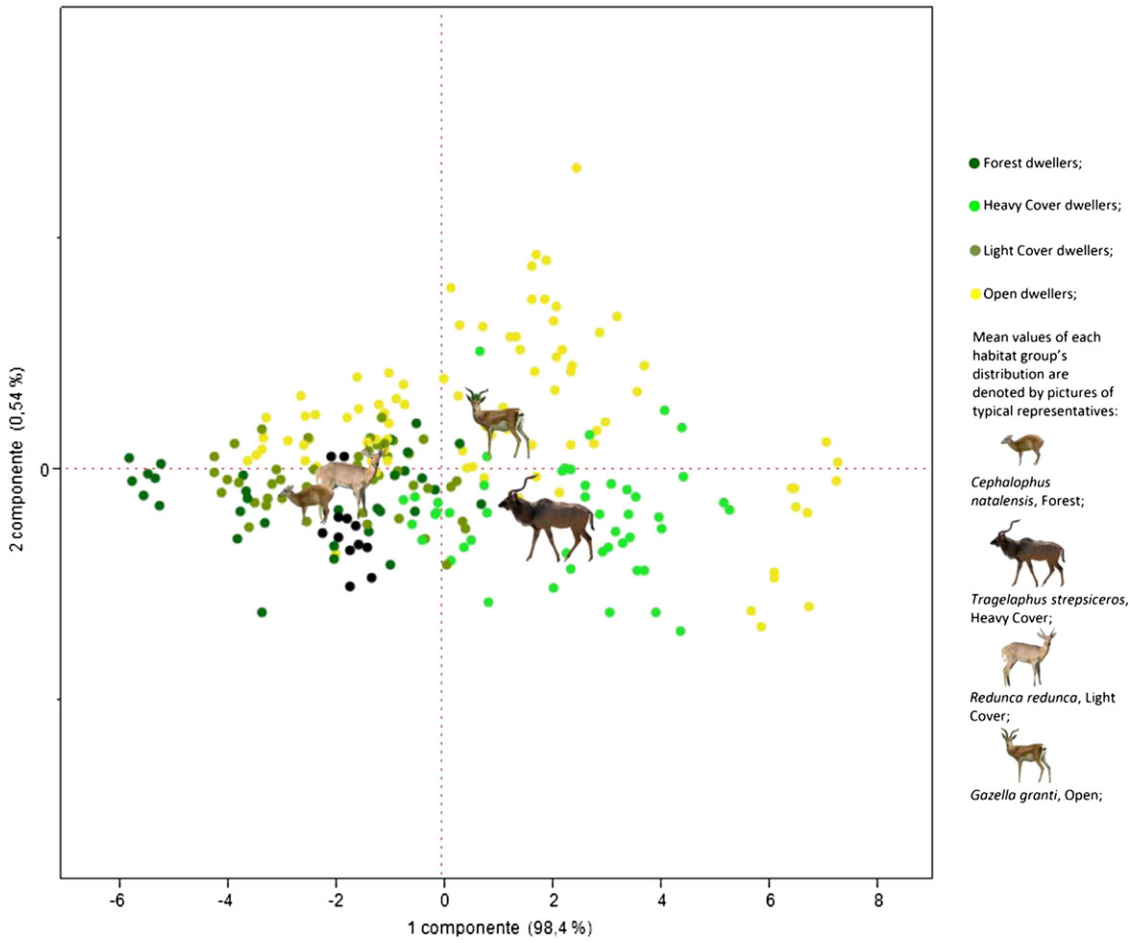


Fig. 10. Results of the PCA analysis for astragali. Specimens of *D. santeng* are denoted by black dots.

the rainforest, did not disappear from the area. Accordingly, at the time of Trinil H.K. Faunal unit, Java was characterized by a heterogeneous landscape with a variety of habitats including open grasslands, swamp forests and relicts of rainforest (Sémah et al., 2010; Sémah and Sémah, 2012). The persistence of relicts of rainforest could be supported by the debated occurrence at Trinil of forest species such as *Pongo pygmaeus* and *Symphalangus syndactylus* (Kaifu et al., 2001; Meijaard, 2004), if confirmed. Nevertheless, the results of a recent study by Smith et al. (2009) would rule out the strongly debated occurrence of *P. pygmaeus* at Trinil, attributing two molars, previously ascribed by some authors (e.g. Kaifu et al., 2001) to this species, to *H. erectus*.

A detailed paleoenvironmental reconstruction of the Trinil site, based on mollusk, fish, bird, reptile and mammal faunas, was done by Joordens et al. (2009). According to these authors the site was likely characterized by near-coastal rivers, lakes, swamp forests, lagoons, and marshes with minor marine influence, laterally grading into grasslands. It was, in terms of local environmental conditions and faunal composition, comparable to the modern tropical freshwater swamp forest biotope (Joordens et al., 2009). Habitat inferred here for *D. santeng*, a forest dweller living in close canopy settings, is coherent with the most recent paleoenvironmental reconstructions of Java at the time of the Trinil H.K. Faunal unit. At that time, this species was widely diffused on the island, inhabiting areas possibly characterized by relicts of rainforest (e.g. Sangiran; see Sémah et al., 2010; Sémah and Sémah, 2012) and unflooded or only seasonally flooded patches of swamp forest (Trinil).

As for paleobiogeography and the time and way of Java colonization from continental mammalian taxa, our results add some evidence that should contribute to shedding light on some debated issues, albeit not solving them. It is well known that at the time of the "*Stegodon-H. erectus* fauna", along with *D. santeng* and the above mentioned large bovids, Java was inhabited by a few species almost identical to their continental relatives, such as *Tapirus indicus*, macaques, pigs, a hippopotamus (*Hexaprotodon sivajavanicus*), deer and several more taxa, as well as *H. erectus* (Mishra et al., 2010; Van der Made, 2011). The affinities between the "*Stegodon-H. erectus* fauna" and the Pinjor fauna from the Siwaliks would indicate, as far as the colonization of Java is concerned, a dispersal via a Siva-Malayan route (De Vos and Long, 2001; De Vos, 1996), but the time of dispersal of endemic taxa, i.e. *Duboisia*, remains doubtful.

As a matter of fact, disentangling factors behind the body size reduction of *D. santeng* with respect to its putative ancestor is not trivial, because its small dimensions might be related to the conclusion that it was a forest dweller, likely inhabiting large relicts of rainforest or patches of swamp forest. According to the Maneuverability hypothesis (see Bro-Jørgensen, 2008), the physical structure of dense habitats would directly select for smaller body size, because the latter reduces obstruction to movement and facilitates concealment. In mammals, there are several examples of sister taxa where the forest taxa is significantly reduced in size (e.g. Africa forest elephant *Loxodonta cyclotis*, (male maximum body mass = 3500 kg) counts for about a 55% of the size of savannah elephant *Loxodonta africana*, (male maximum body mass = 6300 kg); the savannah buffalo forest buffalo *Syncerus caffer nanus*, 320 kg, accounts for about the 38% of the size of savanna buffalo *Syncerus caffer caffer*, 850 kg, Bro-Jørgensen, 2008 and references therein). Therefore, on the one hand, the selective pressures that the environment would have exerted on *D. santeng* has to be taken into account in deciphering its body size reduction. On the other hand, the reduction in size of *D. santeng* seems to be too extreme (S_i values would indicate an average body size reduction of about 70% with respect to *B. tragocamelus*) to be justified only on the basis of dense habitat selection. Therefore, the effects of evolutionary patterns affecting the body size of mammals on islands should also be taken into account. Hence, the hypothesis that *D. santeng* might represent an older endemic settler cannot be rejected. Nevertheless, the claimed occurrence of *D. santeng* in the late Middle Pleistocene of nowadays peninsular Malaysia, that would suggest a more widely diffused range of this species across the Sundaic province, makes this hypothesis fragile. The uncertainty about actual means of the apparent size reduction of *D. santeng*, is further complicated, on the one hand, by its elongated and quite slender metapodials, an unusual feature in typical endemic insular bovid, such as *Myotragus balearicus* from the Balearic Islands (robusticity index = 0.097 for the metatarsal of *D. santeng* 8465; average robusticity index = 0.26 for the metatarsals of *M. balearicus* in Andrews, 1915 Fig. 7), from which *D. santeng* differs in other features peculiarly related to the evolutionary patterns affecting mammals in insular contexts, such as the typical fusion of tarsal bones (Bover et al., 2010). On the other hand, the slenderness of the metapodials of the Javanese boselaphine mirrors the morphological traits of Plio-Pleistocene Sardinian bovids (robusticity index = 0.097 for the metatarsal of *D. santeng* 8465; robusticity index = 0.1 for the metatarsal of *Nesogoral* VI 3 Antica 1045 A Fig. 7), which evolved on the island under the selective pressure of a top predator, the running hyena *Chasmaporthethes melei* (Palombo et al., 2006). This suggests that the moderate cursorial aptitude shown by *D. santeng* would relay with the presence of various predators on Java. In fact, at the time of the Trinil HK faunal unit, the Javanese carnivore guild included a tiger – *Panthera tigris* – and a canid – *Cuon* (*Mececyon*) *trinilensis*. In the subsequent Kedung Brubus faunal level, despite the disappearance of *C. trinilensis*, a marked increase of the predatory pressure was produced by the occurrence of the large hyena *Pachycrocuta brevirostris* (Hertler and Volmer, 2008). Moreover, not only carnivores fed on *D. santeng*, but also reptiles and *H. erectus*, as testified by cut marks observed on long bones recovered in Sangiran (Bouteaux and Moigne, 2010).

5. Remarks

Results obtained stress the usefulness of a multiproxy approach in inferring the paleoecological behavior of fossil taxa. In particular, combined results coming from qualitative and quantitative analysis devoted to inferring dietary aptitude and habitat preferences have been demonstrated as particularly informative. Outputs coming from methods adopted in this study (mesowear, surface texture analysis DASTA, morphology and biometry of selected limb bones, and to a some extent, body size estimate) give results in agreement with each other. All in all, the hypothesis that *D. santeng* was a forest-dweller mostly feeding on leaves and only occasionally on harder vegetation, seems to be fully substantiated. Timing and mode of evolution of *D. santeng* remain still unclear. Whether the bovid evolved under fully insular conditions and its small body size compared to its putative ancestor, *Boselaphus*, should be attributed to the so-called island rule or to an adaptive shift in biotope, or a combination of both factors, remain unanswered questions.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2013.03.012.

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